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# Improved homeothermy and hypothermia in African lions during gestation

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Mammals use endogenously produced heat to maintain a high and relatively constant core body temperature ($T_b$). How they regulate their $T_b$ during reproduction might inform us as to what thermal conditions are necessary for optimal development of offspring. However, few studies have measured $T_b$ in free-ranging animals for sufficient periods of time to encounter reproductive events. We measured $T_b$ continuously in six free-ranging adult female African lions (*Panthera leo*) for approximately 1 year. Lions reduced the 24 h amplitude of $T_b$ by about 25% during gestation and decreased mean 24 h $T_b$ by $1.3 \pm 0.1^\circ$C over the course of the gestation, reducing incidences of hyperthermia ($T_b > 39.5^\circ$C). The observation of improved homeothermy during reproduction may support the parental care model (PCM) for the evolution of endothermy, which postulates that endothermy arose in birds and mammals as a consequence of more general selection for parental care. According to the PCM, endothermy arose because it enabled parents to better control incubation temperature, leading to rapid growth and development of offspring and thus to fitness benefits for the parents. Whether the precision of $T_b$ regulation in pregnant lions, and consequently their reproductive success, will be influenced by changing environmental conditions, particularly hotter and drier periods associated with climate change, remains to be determined.

## 1. Introduction

Reproduction is regarded as a particularly costly period of life, with gestation and lactation often requiring the most resources and potentially leading to energetic trade-offs [1]. Measuring how adult females allocate resources during these phases might help us understand how and why different homeostatic processes are prioritized, particularly under free-ranging conditions which can vary unpredictably and in which resources are limited. We measured the $T_b$ and monitored the life histories of six free-ranging lionesses over a sufficient period to encounter pregnancies—approximately 1 year. During this time, three lionesses experienced pregnancies and gave birth to litters of cubs, and three did not, allowing us to compare $T_b$ patterns in lionesses before, during and after pregnancies, and between lionesses that did, and did not, experience pregnancy.

## 2. Material and methods

We measured the $T_b$ of six adult free-ranging lionesses, by surgically implanting miniature temperature bio-loggers (DST centi loggers, Star Oddi, Gardabaer, Iceland) between the parietal peritoneum and the transversus abdominis muscle. Bio-loggers were removed approximately 1 year later. During our study, three lionesses gave birth to litters of cubs (three cubs each), and three did not. All study animals were monitored frequently by direct observation throughout the study.

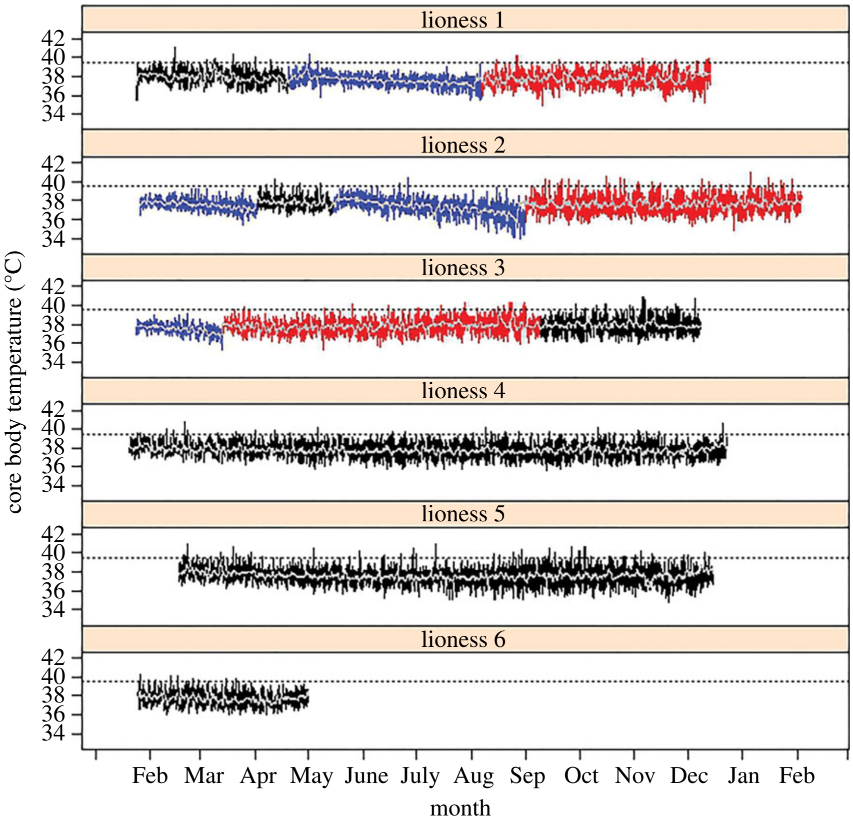

**Figure 1.** Reproductive state and $T_b$ of lionesses. Raw $T_b$ data recorded every 5 min for each lioness included in the study coloured by reproductive state (blue, pregnant; red, lactating; black, non-pregnant and non-lactating). The light grey line indicates the trend in $T_b$. The temperature logger in lioness 6 did not produce reliable data after the beginning of May.

We used the statistics program R [2] and package ‘nlme’ [3] to perform a linear mixed effects analysis of the relationship between 24 h amplitude of $T_b$ and reproductive status. The 24 h amplitude of $T_b$ was defined as the difference between the maximum and minimum 24 h $T_b$. We recognized three reproductive states: pregnant, non-pregnant and lactating. Non-pregnant is taken to mean non-pregnant and non-lactating. We included 24 h dry-bulb temperature range and reproductive status (without an interaction term) as fixed effects in the model. As random effects, we had intercepts for individual. The 24 h amplitude of $T_b$ was likely to be temporally auto-correlated so we included a correlation structure with an autoregressive process of order 1. *P*-values were obtained by likelihood ratio tests of the full model that contained the effect in question (reproductive status), against a null model that did not include the effect in question. We used *multcomp* [4] to perform a *post hoc* multiple variable comparison to determine in which reproductive states 24 h amplitude of $T_b$ differed. Linear mixed effects analysis was also used to determine the relationship between mean 24 h $T_b$ and ‘pregnancy day’ (the number of days into a gestation), and only data recorded during gestation were included in the analysis. We included mean 24 h dry-bulb temperature and pregnancy day as fixed effects, and included individuals as random intercepts, with an autoregressive correlation structure of order 1. Once again, *p*-values were obtained by likelihood ratio tests of the full model with the effect in question (pregnancy day), against a null model that did not include the pregnancy day. Raw data are accessible online [5].

## 3. Results

Mean female 24 h $T_b$ was 37.7 ± 0.1°C (1 s.d. calculated between individual means) outside of pregnancy. Pregnancy day had an effect on mean 24 h $T_b$ ($\chi^2_1 = 58.8$, $p < 0.0001$). In a 108-day gestation, $T_b$ decreased by 1.3 ± 0.1°C (approximately 0.01°C per day, s.d. estimated by model, figure 1). Reproductive status affected 24 h amplitude of $T_b$ ($\chi^2_2 = 106.7$, $p < 0.0001$), which was approximately 25% lower during pregnancy (mean = 1.7 ± 0.3°C) than when females were lactating (mean = 2.4 ± 0.3°C; $z = 10.8$, $p < 0.0001$) or not pregnant (mean = 2.2 ± 0.3°C; $z = 7.9$, $p < 0.0001$). Mean 24 h amplitude of $T_b$ was not different between non-pregnant and lactating ($z = 1.7$, $p = 0.2$) reproductive states. Reduced 24 h amplitude of $T_b$ during pregnancy indicates that lionesses improved homeothermy during pregnancy compared with non-pregnant and non-lactating periods. Incidences of hyperthermia ($T_b > 39.5$°C) occurred less frequently in females during pregnancy than when they were lactating or non-pregnant (figure 1).

## 4. Discussion

Improved homeothermy, and a continuous decline in mean $T_b$, which we refer to as gestational hypothermia [6], appear to be thermal characteristics of gestation in lions. As far as we are aware, our study is the first to demonstrate gestational hypothermia in free-ranging mammals, with mean 24 h $T_b$ 1.3°C lower at the end of pregnancy. Over the same period, there was no change in $T_b$ of non-pregnant lions. The clear trend of decreasing mean $T_b$ in lionesses began in the first trimester (figure 1), earlier than in reports of gestational hypothermia in laboratory animals [7–9]. In addition to the decline in mean $T_b$, pregnant lions also regulated $T_b$ with greater precision over 24 h, with the mean amplitude of $T_b$ 0.6°C lower than that when non-pregnant or lactating.

Gestational hypothermia has been observed in a variety of species under laboratory conditions [7–11], and appears to represent a regulated reduction in $T_b$ rather than an inability to regulate a high $T_b$. The threshold temperature for initiating cooling mechanisms was reduced in pregnant compared with non-pregnant rats, indicating that pregnant rats defended a lower $T_b$ [12]. Pregnant rats, like non-pregnant rats, also did not select a warmer microclimate when it was made available to them [7]. In rats, a central angiotensin $AT_1$ receptor mediated mechanism appears to play a role in generating the gestational hypothermia [11].

The improved homeothermy during pregnancy is likely the result of increased thermoregulatory effort, by a combination of physiological and behavioural mechanisms. Maintaining a narrow 24 h range of $T_b$ during pregnancy requires both food energy and water [13]. The requirement of extra resources makes improving homeothermy a costly process and a Darwinian argument posits that there should be some corresponding gain in fitness, or selection would act against this waste of resources. One advantage of improved homeothermy during gestation might be accelerated offspring development, resulting from rapid cell division occurring in conditions that better approximate the optimum temperature for cell division. For large endothermic mammals that regulate $T_b$ at a high temperature (usually between approx. 36°C and 39°C [13]), further increases in $T_b$ to accelerate offspring development are not feasible. Rather, to accelerate offspring development, large mammals may focus on spending more time at the optimum temperature for development by increasing thermoregulatory effort during gestation, as we see here in lions.

Lions have a particularly strong incentive to accelerate offspring development. Male lions dominate a pride of females for only a short period (about 2 years [14]), during which they must sire and raise cubs to maturity. If cubs have not reached independence by the time incumbent males are forced out, the cubs face a high likelihood of being killed by incoming males [15,16]. The imminent threat of infanticide gives females a strong incentive to achieve rapid fetal development as this will reduce the time between the date on which cub(s) are conceived and the date at which they reach independence. As cubs that reach independence faster are less likely to be exposed to and killed by infanticidal males, this may explain why lionesses invest additional resources to increase thermoregulatory control during gestation.

If rapid fetal development is the primary adaptive advantage of improved homeothermy during gestation, as we suggest, then the presence of improved homeothermy during gestation in lions would support the parental care model (PCM) for the evolution of endothermy. The PCM, as proposed by Farmer [17], seeks to explain the convergent evolution of endothermy as a by-product of more general selection for parental care. According to the PCM, endothermy would have enabled parents to better control incubation temperature, leading to rapid growth and development of offspring and thus to fitness benefits for the parents.

Support for the PCM has been found in tenrecs, primitive eutherian mammals, which were more homeothermic during pregnancy than at other times [18]. Tighter regulation of $T_b$ during near-term gestation has also been demonstrated in echidnas (*Tachyglossus aculeatus*), bats (*Eptesicus fuscus*) and dunnarts (*Sminthopsis macroura*) [19], and more recently support for the PCM has been found in the remarkable discovery of reproductive endothermy in a small (approx. 2 kg) reptile (tegu lizard; *Salvator merianae*) [20,21]. Although data on free-ranging large mammals during reproduction are scarce, if the PCM does explain increased homeothermy during gestation in lions, we might expect to observe it also in other species. However, evidence in the literature is mixed. Bears practise delayed implantation (embryonic diapause) and pregnancy occurs during hibernation [22], making their thermal biology complex. However, free-ranging bears (*Ursus arctos*) also displayed improved homeothermy during the gestation period [22]. In springbok (*Antidorcas marsupialis*), neither homeothermy nor gestational hypothermia was evident in pregnant females [23]. However, the mean 24 h amplitude of $T_b$ in springbok was only 1.2°C, and further decreases in amplitude of $T_b$ may only be possible at a prohibitive cost.

Gestational hypothermia is also likely to facilitate fetal development. Fetal $T_b$ is necessarily higher than maternal $T_b$, because the metabolically active and rapidly dividing fetal cells generate more heat than those of the mother, and fetal $T_b$ has been found to be approximately 0.5°C higher than maternal $T_b$ for all species measured so far [9]. Cell division has been found to cease at temperatures higher than 40°C [24], and developing fetuses are vulnerable to damage by episodes of hyperthermia [25]. Gestational hypothermia therefore might be necessary to protect the fetus from damage caused by episodes of hyperthermia. A lower maternal body temperature may also protect the fetus from hypoxia by reducing metabolism, and therefore oxygen demand in the mother, or by causing a leftward shift in the oxyhaemoglobin dissociation curve—increasing oxygen affinity and saturation as a result [6].

Thermoregulatory responses of free-ranging animals exposed to complex stressors differ from those of captive animals [26], and insights from free-living animals are critical if we are to understand how large mammals might respond to future changing climates [27]. This study highlights the importance of thermoregulatory control and protection from hyperthermia in lions (and potentially other large carnivores) during gestation, and has implications for conservation initiatives. For example, large carnivores living in more extreme future environments may be able to cope with normal daily thermoregulatory demands but might fail to reproduce successfully.

Ethics. The study received approval from the University of Oxford Animal Welfare and Ethical Review Board and the University Veterinary Services Department, and from the Animal Ethics Screening Committee of the University of the Witwatersrand (clearance certificate 2013/54/04).

Data accessibility. Miniature bio-logger temperature data: Dryad, http://dx.doi.org/10.5061/dryad.32nm0 [5].

Authors' contributions. P.D.T. participated in study design, carried out the fieldwork, did the data analysis and drafted the manuscript. A.F. participated in study design, data interpretation and critically revised the manuscript. A.H. participated in fieldwork and data acquisition and critiqued the manuscript. T.H. contributed towards data analysis and interpretation and revision of the manuscript. A.J.L. and D.W.M. contributed to study conception, design and critically revised the manuscript. All authors gave final approval for publication and agreed to be held accountable for the content of this manuscript.

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